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Dry matter and leaf area partitioning, bud fertility and second season growth of *Vitis vinifera* L.: Responses to nitrogen supply and limiting irradiance

by

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S u m m a r y : Potted *Vitis vinifera* L. plants were grown under controlled environmental conditions at five different levels of nitrogen (0, 1, 5, 10, 100 mM NH_4NO_3) in combination with two different levels of irradiance (30 and 140 µmol m^{-2} s^{-1} PAR, respectively) during bloom. The immediate, whole season and second year effects on vegetative growth were assessed, and bud fertility and rate of development were evaluated. The optimum N addition level was 1 mM NH_4NO_3 for root growth and 5 mM for shoot growth, respectively, both after bloom and at the end of the first growing season. This growth response to N supply became apparent only in the higher light treatment and was mainly due to an N-induced enhancement of leaf and lateral shoot growth. Low-light stress also strongly enhanced the number of new leaves and laterals, but total dry matter production was reduced and did not respond to N nutrition. Light restriction increased the specific leaf area by 52 % and the leaf area ratio by 37 % but did not affect the leaf weight ratio. The leaves of N-deficient vines, in particular in combination with light stress, senesced earlier than those of vines with sufficient or excessive N availability. The light effect on shoot growth in the second season was inverted compared with the first season, and the peak response to N supply was shifted towards 100 mM NH_4NO_3. Limiting light conditions during inflorescence initiation severely reduced the bud fertility but advanced the date of bud break and enhanced the rate of development of the new shoots in the subsequent season. The optimum N supply rate for both bud fertility and development was 5 mM NH_4NO_3. Bud mortality was not affected by either treatment factor. These data indicate that the bloom period is critical for reproductive development of grapevines, with high sensitivity to environmental stress. They also emphasize the importance of nutrient reserves in the permanent structure for both compensatory and early season growth.

K e y w o r d s : grapevine, light, nitrogen, bloom, plant growth, compensation, source, sink, bud fertility.

Introduction

The ability of grapevines to maintain active growth under conditions of low soil N or low irradiance may be related to translocation of substrates from older, sequentially senescing leaves and permanent organs to the root or shoot tips (KELLER *et al.* 1995). The direction and destination of recirculation is dependent on the kind of stress. The optimum resource allocation hypothesis states that plants respond to insufficient resource availability by allocating newly acquired carbon (C) to organs that enhance the acquisition of resources most strongly limiting growth (reviewed by BLOOM *et al.* 1985). In general, plants exposed to C limitation often increase partitioning to shoots (BLOOM *et al.* 1985), while plants exposed to nutrient stress typically increase root growth (ROBINSON 1986). Reproductive growth, on the other hand, is often more sensitive to environmental stress or limitation of resources than vegetative growth (CHIARIELLO and GULMON 1991).

Grapevine growth can be characterized by two distinct terms: plant vigor and plant capacity (WINKLER *et al.* 1974). Vigor is defined as the current quality or condition of the vine, which is expressed in the growth rate of the various plant parts. According to HUGLIN (1986), a vine's vigor manifests itself in the total amount of pruning wood, and there is a positive relationship between the pruning weight and fruitfulness. Capacity describes the ability at the start of the growing season for total production during the entire season. In a recent review on nitrogen (N) assimilation and storage, OAKS *et al.* (1991) stated that in perennial plants the amount of new vegetative growth is highly correlated with the levels of C, N and other nutrients stored. Thus, the growth capacity is essentially dependent on the expansion and efficiency of the root system and the condition of reserve and transport organs in order to sustain both vegetative growth and yield potential (quality and quantity). This is supported by an efficient leaf apparatus.

The responses of gas exchange, flower abortion, nutrient uptake, N and C distribution of fruiting pot grown vines exposed to a series of N application levels under light-limited conditions during the flowering period were described in our preceding publications (KELLER and KOBLET 1994, KELLER *et al.* 1995). The objective of the present study was to establish a link between N supply and weather conditions at bloom time in order to optimize C and N utilization and the balance between vegetative and reproductive growth. The combined effects of N supply and light restriction on dry matter partitioning, vegetative growth, bud fertility and regrowth the following growing season were investigated.

Materials and methods

G r o w t h a n d e x p e r i m e n t a l c o n d i t i o n s : Three-year-old pot-grown *Vitis vinifera* L. plants (cv. Müller-Thurgau on SO 4 rootstocks) were chosen for uniformity of growth. The previously unfertilized vines bearing 2 shoots with 2 clusters each were placed in two

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identical rooms of a controlled environment facility (phytotron) on February 1, 1991 and treated as described previously (KELLER and KOBLET 1994, KELLER *et al.* 1995). The experimental treatments consisted of 5 nitrogen (N) application levels, starting 10 d prior to the onset of flowering, and 2 light regimes, beginning at the onset of flowering (April 26). The N levels were 0 (N0), 1 (N1), 5 (N5), 10 (N10), 100 (N100) mM NH_4NO_3, in 2 l of distilled H_2O, replicated on 9 vines for each light condition and applied once a week for 4 weeks.

Photon flux densities in the two light regimes were 140 µmol m^{-2} s^{-1} photosynthetically active radiation (PAR) (moderate light, treatment ML) and 30 µmol m^{-2} s^{-1} PAR (low light, treatment LL) in the respective phytotron rooms. Both treatment factors were imposed till the end of bloom, when 3 plants per treatment combination were sampled (May 15). After sampling, the remaining 6 plants from each treatment were placed in a greenhouse and topped to 12 leaves per shoot. After the danger of spring frost damage was over, these vines were transferred to the field (June 6) for the rest of the current and the subsequent season.

Growth and bud fertility measurements: At the end of bloom the organs of the vines were separated into roots, trunk, spur, main shoots, lateral shoots, main leaves, lateral leaves and inflorescences. Fresh and dry weights (after drying at 65 °C in a forced air oven) were determined. Leaf area was measured using a LiCor Li-3100 area meter (Licor Inc., Lincoln, Nebraska, USA). Specific leaf area (SLA = leaf area per unit leaf dry weight), leaf area ratio (LAR = leaf area per unit whole-plant dry weight) and leaf weight ratio (LWR = leaf dry weight per unit whole-plant dry weight) were calculated. The pruning weights were recorded in the following winter upon pruning to one 4-bud spur per plant. The N concentration in the pruning wood was determined as described by KELLER *et al.* (1995).

For the evaluation of bud fertility and regrowth, the main shoots were cut to single-node cuttings after pruning weight was recorded. The cuttings were placed in a water bath to force into growth, following the procedure of CANDOLFI-VASCONCELOS and KOBLET (1990). After 13 and 27 d, respectively, the rate of bud development was evaluated in terms of phenological stages as defined by EICHHORN and LORENZ (1977). In addition, bud mortality, the number of inflorescences per bud and fresh weights of the new shoots were recorded, and the chlorophyll content of the first fully expanded leaf on the new shoots was determined non-destructively using a portable dual-wavelength SPAD-502 chlorophyll meter (Minolta Camera Co. Ltd., Osaka, Japan). For calibration, a polynomial regression was computed between LCD (liquid cristal display) readings and extractable chlorophyll content per unit leaf area (Chl = Chl_a + Chl_b) determined as described by CANDOLFI-VASCONCELOS and KOBLET (1991). The equation resulting from a sample of 40 leaves from field-grown Müller-Thurgau vines (each value representing the mean of five individual measurements on the same leaf) was:

Chl (mg dm^{-2}) = 0.0006 $[LCD]^2$ + 0.017 [LCD] + 0.408 ($r = 0.98$, $P < 1$ %);

within a range of 0.8 to 2.3 mg dm^{-2}, in young and mature leaves.

In the season following imposition of the stress treatments, the vines were trained in the same way as in the first season. After bloom, each of 2 shoots was topped to 12 leaves, and the laterals from the shoot base to the upper cluster (fruiting zone) were removed. Fresh and dry weights of these shoot tips and laterals were determined and used as an estimate of second season growth.

Table 1

Effect of irradiance and N application during bloom on the leaf growth of potted grapevines in the phytotron. Values are means ± SE (n = 3). Within a column section, means followed by the same letter are not significantly different at P < 5 %

NH_4NO_3	total leaf area dm^2	main-leaf area dm^2	area/main leaf dm^2	number of main leaves	water content % fw	SLA dm^2 g^{-1}	LAR cm^2 g^{-1}	LWR g g^{-1}
30 µmol m^{-2} s^{-1} PAR (treatment LL)								
0 mM	28.35±0.71 a	25.42±0.65 a	1.19±0.01 a	21.3±0.7 a	86.4±0.7 ab	3.55±0.26 ab	55.3±3.7 bc	0.16±0.002 a
1 mM	28.72±2.31 a	25.80±1.72 a	1.19±0.05 a	21.7±0.9 a	87.7±0.6 a	3.97±0.20 a	54.6±4.3 c	0.14±0.013 a
5 mM	35.36±4.11 a	29.99±3.31 a	1.30±0.08 a	23.0±1.2 a	85.9±0.8 ab	3.58±0.18 ab	69.5±5.8 ab	0.20±0.023 a
10 mM	32.47±1.84 a	27.01±1.10 a	1.29±0.07 a	21.0±0.6 a	86.4±0.5 ab	3.59±0.22 ab	70.5±2.9 a	0.20±0.019 a
100 mM	29.01±2.25 a	25.22±0.90 a	1.20±0.02 a	21.0±0.6 a	84.3±0.9 b	2.90±0.21 b	56.7±4.6 abc	0.20±0.024 a
[a]	30.78±2.67 *	26.69±1.86 n.s.	1.23±0.05 *	21.6±0.8 **	86.1±0.9 **	3.52±0.28 **	61.3±5.6 **	0.18±0.021 n.s.
140 µmol m^{-2} s^{-1} PAR (treatment ML)								
0 mM	19.84±0.66 c	18.90±0.80 c	1.23±0.04 a	15.3±0.3 b	80.4±1.6 a	2.29±0.18 a	34.5±1.4 c	0.15±0.018 b
1 mM	25.69±2.12 abc	23.70±1.70 abc	1.33±0.13 a	18.0±0.6 ab	81.0±1.1 a	2.36±0.14 a	39.4±1.7 c	0.17±0.016 ab
5 mM	34.60±1.26 a	29.77±0.64 a	1.54±0.04 a	19.3±0.3 ab	81.0±0.6 a	2.39±0.07 a	54.2±1.4 a	0.23±0.003 a
10 mM	30.90±5.82 ab	27.85±4.71 ab	1.24±0.06 a	22.3±2.8 a	80.0±1.2 a	2.39±0.20 a	51.5±1.2 ab	0.22±0.017 a
100 mM	22.69±2.52 bc	20.18±2.06 bc	1.30±0.18 a	16.0±2.3 b	81.1±0.3 a	2.16±0.07 a	43.2±6.8 bc	0.20±0.028 ab
	26.74±4.12	24.08±3.27	1.33±0.11	18.2±2.1	80.7±0.9	2.32±0.13	44.6±5.2	0.19±0.023

[a] Means between light regimes differ at **P < 1 %, *P < 5 % or n.s. do not differ significantly

The data were subjected to Bartlett's test to check homogeneity of variance and subsequently to analysis of variance and F-test. Duncan's multiple range test was used to check differences between means. Selected parameters were examined using correlation and polynomial regression analysis. All statistical tests were performed on WIDAS (Wissenschaftlich Integriertes Daten-Auswertungs-System, MSI Dr. Wälti AG, Switzerland).

Results

Both N availability and light conditions altered C partitioning to the various organs of the vine (Fig. 1). Inflorescence dry weight was most severely reduced by limiting irradiance (-31 %), followed by the leaves (-23 %), roots (-17 %), shoots (-16 %) and the trunk (-10 %). Only under moderate irradiance, dry mass partitioning was significantly affected by N supply (Fig. 1); N deficiency enhanced root growth, whereas at high N availability root growth dropped to the level of LL. Dry matter partitioning to the wood (trunk and spur) followed the same pattern as to the roots, though less pronounced.

Carbohydrate partitioning to the 'structural parts' of the grapevine appears to be favoured under high light/low N conditions and depressed under low light/high N conditions, the other combinations being intermediate. Dry matter accumulation in the shoots followed an optimum pattern in ML, with a maximum at 5 mM NH_4NO_3, whereas

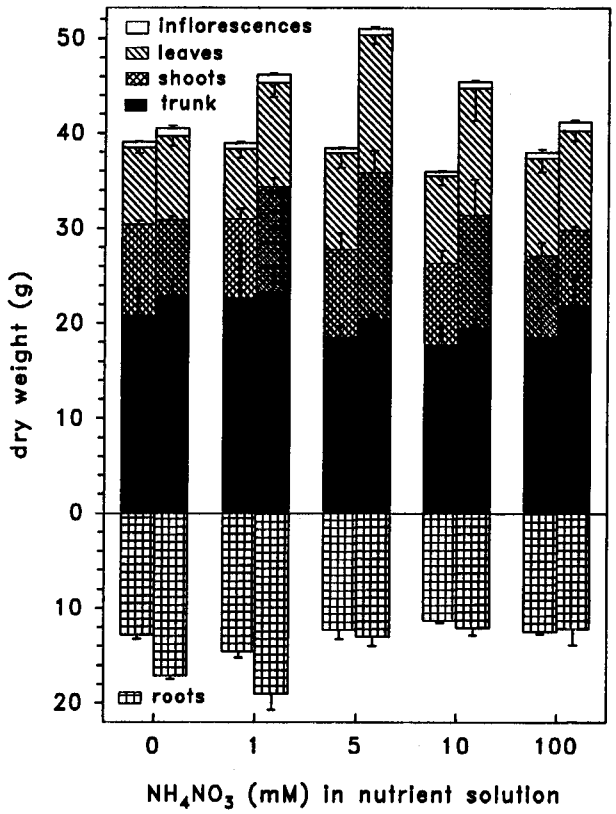

Fig. 1: Effect of irradiance and N application during bloom on dry weight partitioning of potted grapevines in the phytotron. Left bar of each pair: treatm. LL, 30 µmol m^{-2} s^{-1} PAR; right bar: treatm. ML, 140 µmol m^{-2} s^{-1} PAR. Values are means + or - SE (n = 3).

no N influence was found in LL. Yet, the LL vines accumulated more fresh weight than the ML vines, since water contents were increased in all organs (data not shown). The response of the root:shoot ratio was very inconsistent, due to large variances. Nevertheless, the ratio was most elevated at a combination of low N availability and moderate irradiance.

The effects of N nutrition and light restriction on leaf growth are presented in Tab. 1. In LL, the water content of the leaves was considerably higher than in ML. The N level failed to alter the water content, except for N100, where it was significantly reduced. Light limitation also strongly increased the SLA, indicating that individual leaves were larger but thinner. Leaf area measurements, however, led to a contradictory result: the main leaves were larger in ML than in LL, whereas the lateral leaves were of the same size in both light regimes. The reduced dry weight of the LL leaves therefore accounted for the increase in SLA. Nevertheless, total leaf area per vine was 13 % smaller in ML, and maximum leaf growth (number and size) was observed at N5, regardless of the light regime. The response of total leaf area to added N was brought about by variations in the number of leaves on both the main and lateral shoots and in the number of lateral shoots (Tab. 1, Fig. 2). In the ML treatment, the regression between N level (in mM NH_4NO_3) and number of laterals (n.l.)was:

$n.l. = -0.0075\ N^2 + 0.774\ N + 7.10$ ($r = 0.72$, $P < 1$ %).

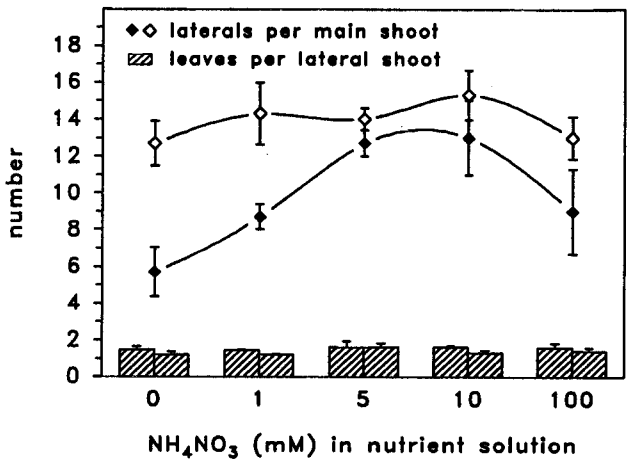

Fig. 2: Effect of irradiance and N application during bloom on the growth of lateral shoots of potted grapevines in the phytotron. Left bar of each pair, open symbols: treatm. LL, 30 µmol m^{-2} s^{-1} PAR; right bar, full symbols: treatm. ML, 140 µmol m^{-2} s^{-1} PAR. Values are means ± SE (n = 3).

The LAR reached a maximum between N5 and N10 in either light regime. The LL vines produced a larger number of leaves and lateral shoots than the ML vines (Tab. 1, Fig.2). Consequently, the LAR was 37 % higher in LL than in ML at all N application levels, indicating a higher ratio of photosynthetically assimilating to non-assimilating tissues under conditions of low-light stress. The response of the LWR to N fertilization was similar to that of the LAR. There was, however, no significant light effect on LWR.

Light restriction, particularly in combination with N deficiency, accelerated senescence of the basal leaves in

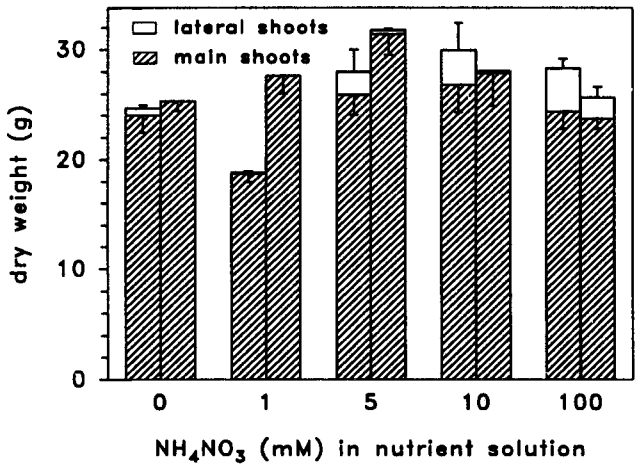

Fig. 3: Effect of irradiance and N application during bloom on the pruning weight of potted grapevines. Left bar of each pair: treatm. LL, 30 µmol m^{-2} s^{-1} PAR; right bar: treatm. ML, 140 µmol m^{-2} s^{-1} PAR. Values are means + or - SE (n = 3).

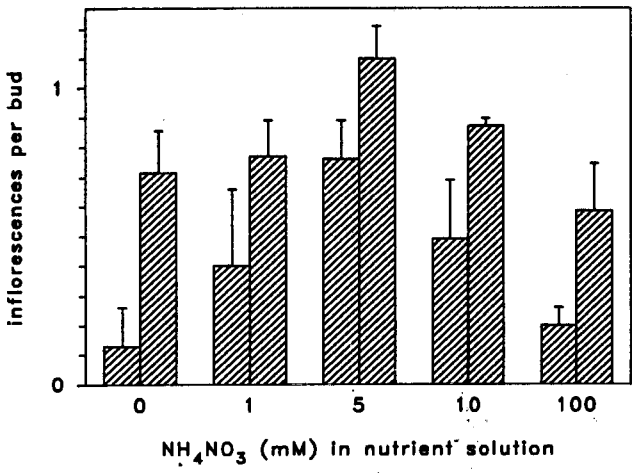

Fig. 4: Effect of irradiance and N application during bloom on the bud fertility of potted grapevines in the second season. Left bar of each pair: treatm. LL, 30 µmol m^{-2} s^{-1} PAR; right bar: treatm. ML, 140 µmol m^{-2} s^{-1} PAR. Values are means + SE (n = 3).

the fall, whereas abscission was delayed when the vines had been supplied with high rates of N during flowering (data not shown). The N100 plants, especially those that had been exposed to the ML regime at bloom, still showed dark green leaves, after the leaves of medium- and low-N plants had been shed. The N effect was less pronounced in the LL vines, where cane maturity was delayed, compared with ML. The pruning weights in the following winter confirmed the results obtained from the sampling after bloom (Fig. 3). In either light regime, maximum growth had occurred between N5 and N10. The main shoots of the LL vines grew significantly less during the entire season than those of the ML vines at all N supply levels, except for N100. However, total pruning weights were not affected by bloom-time irradiance level, because the laterals had compensated for the low-light depression of main shoot growth.

On average, 10 buds unfolded from each shoot in the following spring. Neither treatment factor affected the per cent bud burst and, hence, bud mortality (Tab. 2). How-

Table 2

Effect of irradiance and N application during bloom on regrowth of potted grapevines in the second season. Values are means ± SE (n = 3). Within a column section, means followed by the same letter are not significantly different at P < 5 %

NH_4NO_3	N in pruning wood (% dw)	bud burst (%)	growth stage[a]	new growth (g fw)	chlorophyll mg dm^{-2}
30 µmol m^{-2} s^{-1} PAR (treatment LL)					
0 mM	0.93±0.02 b	93.9±3.03 a	10.0±0.12 a	9.45±0.48 a	0.90±0.05 b
1 mM	0.88±0.04 b	84.9±3.03 a	9.5±0.14 a	6.89±1.09 b	0.91±0.08 b
5 mM	0.89±0.02 b	87.9±8.02 a	9.5±0.13 a	9.11±0.59 ab	1.04±0.02 ab
10 mM	1.08±0.06 a	93.9±3.03 a	9.3±0.43 a	9.52±0.93 a	1.13±0.02 a
100 mM	1.06±0.04 a	90.9±5.25 a	9.3±0.09 a	8.58±0.32 ab	1.15±0.03 a
[b]	0.97±0.06 n.s.	90.3±4.64 n.s.	9.5±0.24 **	8.71±0.85 *	1.03±0.08 n.s.
140 µmol m^{-2} s^{-1} PAR (treatment ML)					
0 mM	0.70±0.06 c	87.9±3.03 a	7.9±0.41 a	6.55±0.94 a	0.81±0.05 c
1 mM	0.76±0.08 c	87.9±3.03 a	8.1±0.49 a	6.64±0.96 a	0.92±0.04 bc
5 mM	0.93±0.02 b	93.9±3.03 a	9.2±0.45 a	8.94±0.17 a	1.03±0.04 ab
10 mM	0.98±0.03 b	93.9±3.03 a	8.5±0.26 a	8.44±0.96 a	1.08±0.03 a
100 mM	1.28±0.04 a	87.9±3.03 a	8.7±0.36 a	7.44±0.38 a	1.09±0.05 a
	0.93±0.13	90.3±3.12	8.5±0.43	7.60±0.86	0.99±0.07

[a] phenological stages (EICHHORN and LORENZ 1977) after 13 days of forcing

[b] Means between light regimes differ at **P < 1 %, *P < 5 % or n.s. do not differ significantly

ever, in the ML treatment the vines had initiated twice as many flower clusters per bud as compared to those in LL (Fig. 4) where the inflorescences were partially replaced by tendrils.

Many of the shoots arising from cuttings of the LL plants were sterile. The buds of the LL cuttings broke about one week earlier, and during the early stages of development, new growth was significantly ahead of that emerging from the ML cuttings, leading to higher shoot fresh weights (Tab. 2). The previous season N5 level appeared to be the optimum for bud fertility (in terms of inflorescences per bud) as well as bud development (in terms of phenological stage) in either light regime, and the N effect was more pronounced in sprouts originating from cuttings from the former ML treatment.

Regrowth fresh mass was positively related to total pruning weight of both LL ($r = 0.69$, $P < 1$ %) and ML ($r = 0.75$, $P < 1$ %) vines, while no significant relation was found to the N concentration in the pruning wood. However, a multiple correlation of regrowth with both total pruning weight and N concentration revealed $R = 0.73$ ($P < 1$ %) in LL and $R = 0.80$ ($P < 1$ %) in ML. The chlorophyll content in the first new leaf was directly related to the N concentration in the pruning wood in both LL ($r = 0.72$, $P < 1$ %) and ML ($r = 0.75$, $P < 1$ %). A multiple correlation of Chl with both N concentration and pruning weight even gave a correlation of $R = 0.80$ ($P < 1$ %) in LL and $R = 0.79$ ($P < 1$ %) in ML. After bloom, shoot growth of the former LL plants still slightly exceeded that of the ML plants, and second year growth was strongly influenced by the soil N level during the previous season bloom period (Fig. 5).

When data from both light regimes were combined, the following equation originated from regression analysis for N (mM NH_4NO_3) and dry weight of shoot tips and laterals (d.w. in g) after bloom:

$$\text{d.w.} = -0.0046\ N^2 + 0.511\ N + 5.041$$

($r = 0.66$, $P < 5$ %).

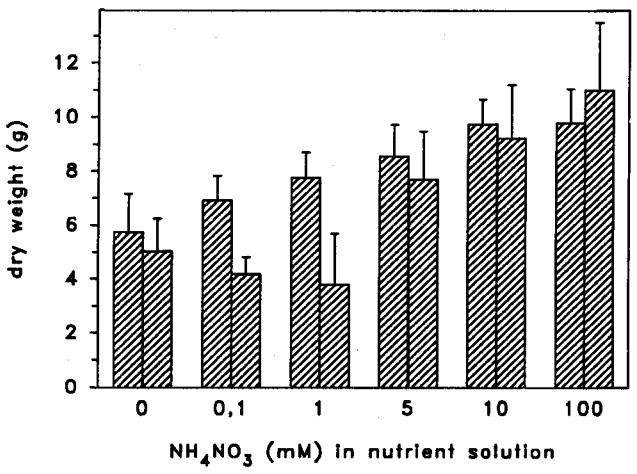

Fig. 5: Effect of irradiance and N application during bloom on second season growth (total of removed shoot tips and laterals after bloom) of potted grapevines. Left bar of each pair: treatm. LL, 30 µmol m^{-2} s^{-1} PAR; right bar: treatm. ML, 140 µmol m^{-2} s^{-1} PAR. Values are means + SE (n = 6).

Discussion

The present experiment showed that N availability may considerably alter both the vigor and growth capacity of grapevines even under moderate light conditions. All organs of the vine were affected. The data from the ML regime are consistent with earlier measurements made by ALLEWELDT *et al.* (1984) under saturating irradiance where "optimum" N supply for vegetative growth was between 0.2 and 1.1 g N per vine, corresponding to our N1 and N5 treatments, respectively. Unexpectedly, the growth response to N addition in ML was not related to net photosynthesis per unit leaf area, which was measured on the same plants (KELLER and KOBLET 1994). Yet, the vine's photosynthetic capacity is also a function of its active leaf area, and N availability primarily affected the number of leaves, rather than their size or photosynthetic rate. The subsequent increase in total leaf area per vine was therefore responsible for the observed N effect on whole-plant dry weight accumulation. Under severe light restriction, however, the response of biomass production to N application was notably less pronounced than in moderate light, and thus, only the capacity may have been affected by N nutrition. The C substrates needed for compensatory leaf formation must have been supplied by respiratory processes, since photosynthetic CO_2 fixation was negligible under conditions of severe light limitation (KELLER and KOBLET 1994). The growth of annual organs was inversely related to the level of wood and root reserves (KELLER *et al.* 1995), supporting the hypothesis that reserves had been remobilized to maintain active growth of the vegetative parts of the vine and that the rate of remobilization was influenced by N nutrition under moderate light conditions. It appears that net C gain, rather than the net photosynthetic rate, is maximized not only over the lifetime of a single leaf, as proposed by MOONEY and GULMON (1979), but also over the whole plant. Grapevines may be able to evolve a range of adaptive mechanisms in response to low irradiance that trigger the production of new leaves rather than maintenance of the source capacity of mature leaves. In addition, there is a redirection of assimilate and reserve partitioning in response to stress situations. This is also illustrated by the reaction of the LAR to the two treatment factors.

The increase in the number of meristematic tissues due to the elevated number of expanding main and lateral leaves in response to applied N or low-light stress led to an increase in sink activity of the shoot tips, decreasing the availability of carbohydrates for translocation to roots and inflorescences. As early as 1883, MÜLLER-THURGAU (cited by SARTORIUS 1926) suggested that the poor fruit set occurring during cool, overcast weather was due to starvation of the grape flowers because of limited photosynthesis and translocation, and this was aggravated by the competitive effect of numerous, rapidly growing shoot tips.

Light restriction and heavy N nutrition clearly enhance allocation of carbohydrates and nutrients to the growth of annual vegetative organs at the expense of reproductive and perennial plant parts, although at extreme soil N levels shoot growth is decreased, too. The restricted root dry

mass of the vines in the LL regime is consistent with data obtained by ARAUJO and WILLIAMS (1988), who stated that root growth is only possible when excess photoassimilates are available from the shoots. The proportion of C that is partitioned to roots is determined by the amount of sucrose that is produced in the leaves (HUBER 1983). Under low-light stress assimilates are partitioned preferentially to starch rather than sucrose, and during the night daily carbohydrate reserves of source leaves are utilized primarily for shoot growth (MOONEY and WINNER 1991). On the other hand, ÅGREN and INGESTAD (1987) suggested that the root:shoot ratio is inversely related to the internal N concentration. If the restriction in shoot growth resulting from low tissue N concentrations exceeds the decline in photosynthesis, which apparently was the case in the ML regime (KELLER and KOBLET 1994, KELLER *et al.* 1995), C is preferentially allocated to the roots (RUFTY *et al.* 1988). Thus, under conditions of N deficiency the roots have priority over available N. This reaction could, however, only be observed in the ML treatment.

Interestingly, after deducting the amount of non-structural carbohydrates (as determined by KELLER *et al.* 1995) from the total dry weight of the trunk and roots, respectively, the light effect on the remaining dry matter disappeared, while the N effect was not modified. This indicates that there are non-structural N-containing compounds present in the permanent tissues, which are not affected by the light environment. Part of these compounds may have been remobilized to compensate for the insufficient N present in the root zone.

The elevated water content in all organs of the LL vines may be due to the strong decrease of total daily irradiance. The higher photosynthetic activity in ML (KELLER and KOBLET 1994) implies an increased water demand for tissue cooling, which could only be achieved by an increased evaporative water loss. The effects of low irradiance on the SLA and LAR were essentially the same as those reported by SCHULTZ (1989) for Riesling grapevines. These data indicate that less structural material per unit area is accumulated in the leaves in response to low-light stress, implying an immediate increase in the investment in photosynthesizing leaf area rather than in dry weight gain. An inverse correlation between irradiance and SLA has also been found by GULMON and CHU (1981), but the close relationship between leaf N concentration and SLA described by these authors could not be confirmed for the sub-optimal light intensities used in our investigation. From the decrease in dry matter production and the simultaneous increase in total leaf area of the LL plants it can be concluded that low-light stress strongly confined the net assimilation rate during the course of the experiment. As a result, the low efficiency of the leaf apparatus led to a transitory decrease in vine vigor.

The strong impact of both light and N on growth and reserve status of the permanent parts of the vine and, hence, on its capacity, imply that, in the long term, effects on both vegetative and reproductive growth are to be expected, if the reserves cannot be replenished during the rest of the season. Carbohydrate or nutrient depletion both can limit regrowth in the following year (reviewed by DICKSON and ISEBRANDS 1991, OAKS *et al.* 1991). Yet, the light-stress-induced increase in the number of new leaves on the LL vines may have enhanced total canopy source capacity subsequent to release from the stress, favoring replenishment of the reserves used to produce these leaves. In addition, the LL plants were severely affected by inflorescence necrosis (KELLER and KOBLET 1994), resulting in restricted investment into reproductive organs in favour of the vegetative organs after flowering. Consequently, there were no differences in total pruning weights and N contents in the pruning wood among the light treatments. The earlier bud break and the faster rate of development of the former LL vines in the second season may, thus, be attributed to elevated reserve status in the one-year-old wood. The close correlations of regrowth and chlorophyll content, respectively, with pruning weight and N content also emphasize the importance of nutrient reserves in the wood for early growth. However, there was a much greater influence of pruning-wood N content on new-growth chlorophyll content than on fresh mass or the rate of development. This indicates that reserve-N is preferentially invested in the buildup of an efficient photosynthetic apparatus rather than evolution of new leaves. This may advance the transition of these leaves from sinks to sources and, therewith, the correlation between N supply level and the weight of shoot tips and laterals after bloom the following season. In grapevines from 30 to 40 % of the N found in current season growth is derived from reserves (WILLIAMS 1991).

Severe reductions in bud fertility by artificial shading of grapevines during the period of inflorescence initiation were also observed by MAY and ANTCLIFF (1963), and BUTTROSE (1970) found that the number of bunch primordia per bud increased with increasing light intensity. PÉREZ HARVEY and VALDÉS LAURSEN (1989) reported a decrease in bud burst and fruitfulness with increasing levels of shading, and the N effects in their study were comparable to our results. Moreover, the response to N supply in this experiment was essentially the same as that reported by KLIEWER and COOK (1971) for saturating irradiance. These data demonstrate that an optimum supply of N is necessary for maximum inflorescence initiation even under sub-optimal light conditions during the critical bloom period. Nevertheless, it is somewhat surprising that N application affected the production of fruitful buds in the LL regime, where no other parameter measured responded to N availability. Regardless of the light level, excessive N availability enhanced the allocation to second year vegetative growth at the expense of reproductive growth, which was also described by SARTORIUS (1968). Our data emphasize the impact of both irradiance and N nutrition during bloom on the partitioning of substrates to competing sinks with different relative priorities.

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